Organization of Saccade Related Neurons in Monkey Superior Colliculus

Robert H. Wurtz, Laboratory of Sensorimotor Research, NEI, Bethesda, MD, USA, and Douglas P. Munoz, MRC Group in Sensory-Motor Physiology, Queen’s University, Kingston, Ontario, Canada.

Introduction

Neurons in the intermediate layers of the monkey superior colliculus (SC) discharge before the onset of saccadic eye movements (for review, see Sparks and Hartwich-Young 1989). The increased discharge rate of these saccade-related cells precedes saccades made to points within the the visual field referred to as the movement field of the cell (Wurtz and Goldberg 1972). The central region of the movement field has the maximal discharge and a gradient of response that fades away as the saccade is made to parts more remote from this central area.

Recent experiments (Munoz and Guittion 1989; Munoz and Guittion 1991; Munoz et al. 1991) have emphasized several characteristics of movement related cells in the cat not previously observed in the monkey (SC). In this brief report we would like to outline recent observations on the monkey (SC) related to both the generation of saccades and the control of fixation. This summary is based upon recent more complete reports (Munoz and Wurtz 1993a; Munoz and Wurtz 1993b; Munoz and Wurtz 1994a; Munoz and Wurtz 1994b).

Two Types of Saccade-Related Cells

We have distinguished two types of saccade cells in the intermediate layers of the SC. One type of neuron, a burst cell, discharged a high frequency burst of action potentials immediately prior to saccade onset. The second type of saccade-related cell had a slow buildup of activity in addition to movement-related activity, and we refer this type of neuron as a buildup cell.

We distinguished the two classes of saccade cells by using several different saccade tasks including the visually guided saccade task in which the monkey made a saccade to a visual target that comes on as the fixation point goes off (Fig. 1). The left column of the figure shows the cell activity aligned on the onset of the visual target and the right column shows the same discharge aligned on the onset of the saccade. Both the burst cell (Fig. 1A) and the buildup cell (Fig. 1B) began to discharge between 60-70 ms after target onset (Fig. 1 left), and then generated a more vigorous discharge in association with saccade onset (Fig. 1 right). The burst cell had a brief pause between the presumed initial visual response and movement-related activity, but the buildup cell lacked any such pause.

In order to determine whether the discharge of the buildup cell was related to the preparation for the saccade or to the presence of the visual stimulus, we also used a memory-guided saccade paradigm in which the monkey had to make a saccade to the spatial location of a briefly flashed target when the fixation point went off. The burst cells showed only a weak response to the target flash and then gave a burst of activity beginning before the onset of the saccade. The buildup cells increased their activity
from the time of the flash until the saccade was made even though the target was no longer visible. In a gap saccade paradigm, the fixation point went off leaving a period of darkness preceding target onset. The buildup cell was silent until after the fixation point went off and then began to discharge in the period of darkness even though the target had not yet appeared. The sustained discharge, therefore, was not simply the result of retinal stimulation since the discharge occurred before the onset of the visual target. In contrast, the burst cell remained silent during the period of darkness between fixation point offset and target onset, and then discharged a brief phasic burst after target onset followed by the more robust burst of spikes synchronized with saccade initiation.

There is a continuum of cell types extending from those with burst cell characteristics to those showing the buildup of activity, but we have divided cells into these two groups. We classified neurons as burst cells if they lacked continuing activity in the interval between the visual and movement related bursts seen in the visually-guided task and during the delay period in the memory-guided tasks. We classified neurons as buildup cells if they had a continuing response between onset of the signal that a saccade was to be made and the saccade related response.
A burst cell discharged maximally for saccades that were close to the optimal amplitude, and when saccade amplitude was greater or less than the optimal, the discharge of the cell diminished. The saccade-related responses of a buildup cell diminished if either the amplitude of the saccade was smaller than optimal or the direction deviated from optimal, but buildup cells continued to discharge for saccades of optimal direction whose amplitudes were greater than the optimal. Therefore, burst cells had movement fields that were closed, that is, the response fields had both proximal and distal borders, whereas buildup cells had open-ended movement fields.

Burst and buildup cells were usually found at different depths below the collicular surface. We determined the depth of each cell relative to the depth of the first multicell visual responses that we encountered on that penetration as the electrode entered the superficial-most layers of the SC. Visual cells, lacking saccade-related activity, were located in about the first mm of the SC; burst cells were found immediately beneath the visual cells; buildup cells were located ventral and somewhat interleaved with the burst cells. Both types of saccade related cells were in the SC intermediate layers.

**Fixation Cells in Rostral Superior Colliculus**

Some cells in the rostral pole of the SC do not increase their discharge rate before saccades but instead do so during periods of active fixation. These cells were first reported in the SC of the cat (Munoz and Guittton 1991; Munoz et al. 1991). Figure 2 shows the discharge of such a fixation cell while the monkey was looking about in the experimental room and then after it made a saccade to the visual target. In Fig. 2A, the raster of neuronal activity is aligned on this onset of the target while in Fig. 2B it is aligned on the time when the monkey fixated on the target. The discharge rate of the cell went up with acquisition of the target, not with target onset. In addition, the discharge was low while the monkey fixated a point on the blank screen but increased with active fixation of the target.

Fixation cells also pause during saccades between actively fixated targets. Just as the duration of saccades increase with saccade amplitude, the duration of the pause also increases with larger saccadic amplitudes. Thus the fixation and the saccade cells have patterns of discharge that are reciprocal. Fixation cells are active during fixation and silent during saccades. Saccade cells are silent during fixation but burst at the time of the saccades.

The discharge of fixation cells was not simply the result of the visual stimulus falling on the foveal receptive field of a visually sensitive neuron since when we blinked the target off briefly, but the monkey continued to fixate, the cell continued to discharge. We have used this continued discharge as a criteria for the identification of fixation cells. Other cells lying more dorsal in the SC to fixation cells do have a pause in their discharge with removal of the fixation point indicating that their response during fixation is a visual one.

We therefore find three types of cells in the SC whose activity is modified in association with the generation of a saccadic eye movement: a burst cell, a buildup cell and a fixation cell. The activity of fixation cells began to decrease as the buildup cell activity increased. The depth of the fixation cells was comparable to that of the buildup cells; they were both located in the deeper intermediate layers directly below the burst cells. Because of both these temporal and the depth relationships, we regard the fixation cells as buildup cells for saccades of zero amplitude.
Figure 2. Example of the discharge of a fixation cell during active fixation. The raster is aligned on the time when the eye entered the computer controlled fixation window. The traces shown from top to bottom are the individual rasters, the spike density function (spden), and the horizontal (Eh) eye position traces. (After Munoz and Wurtz 1993a).

Interaction Between Fixation and Saccades

The reciprocal activity between saccade and fixation cells suggests that they might mutually inhibit each other. This mutual inhibition also suggests that if the activity of the fixation cells were artificially altered, the frequency of the saccades might be changed. We therefore both increased and decreased the activity of the fixation cells in order to test the effect of this on the generation of saccades. We first increased the activity in the fixation zone by applying low frequency electrical stimulation to increase activity of cells adjacent to the site of stimulation. According to our hypothesis, this
manipulation should lead to decreased activity in the saccade zone of the SC.
During a long duration, low frequency train of stimulation (500 ms, 150 Hz, 30 μA) we
found that the monkey could only generate the saccade to a target after the electrical
stimulation ceased. All centrifugal and centripetal saccades were affected. However,
after the delay in initiation, the saccades reached the target. When we applied
stimulation to the fixation zone during the saccade, saccades were interrupted in
midflight. In contrast, when the electrode was outside of the SC area where fixation
cells were recorded, the effect was not evident. When we stimulated at locations above,
below, or rostral to the location of fixation cells with similar parameters, no effect was
seen on saccade generation.

While electrical stimulation allowed us to increase activity within the fixation zone,
injection of GABAAergic drugs allowed us to either increase the activity with a GABA
agonist (bicuculline) or to decrease activity with a GABA agonist (muscimol). We
found that bicuculline and muscimol injections had a marked effect on the monkey’s
ability to fixate a target and make saccades to a new target. Application of bicuculline
increased saccade latencies while muscimol reduced latencies and led to instability of
fixation.

Many of the short latency saccades triggered after muscimol injection occurred within a
latency of 80-100 ms after the target light flashed. Such a short regular latency is
characteristic of express saccades previously observed in the monkey (Fischer and Boch
1983). Of particular relevance to the fixation cells in the SC, is the proposal (Fischer
1987) that express saccades occur most frequently when fixation has already been
broken which is exactly what we propose is the consequence of the functional removal
of the rostral SC with muscimol.

**Buildup Cells are Spatially Related to Saccades**

A salient distinction between burst cells and buildup cells in the SC is a difference in
the pattern of activity in the cells lying at different positions on the SC motor map.
Figures 3 and 4 illustrate this by showing the normalized spike density profiles of cells
in each of the burst and buildup cell layers for 50° saccades. The cells had different
optimal saccade amplitudes and were located in different regions within the SC. The
caudal most cells in both layers had their peak discharge occurring around the time of
saccade onset. In the burst cell layer (Fig. 3), only cells in the caudal SC discharged
with the 50° saccade, and cells lying more rostral to the initially active zone remained
silent. The level of discharge of burst cells in the initially active zone simply
diminished so that by saccade termination, these neurons were almost silent. However,
the buildup cells lying rostral to the initially active cells were activated sequentially at
some point during the 50° saccade (Fig. 4). Looking at the left column in Fig. 4, where
cell responses are aligned on saccade onset, the peak discharge began before the 50°
saccade for the caudal most cell and gradually moved later for more rostrally located
cells. A clear moving front of activity is therefore visible beginning in the caudal SC
and moving to the rostral SC. Again, looking at the burst cell layer no such movement
is evident.

In the rostral SC, activity was confined to the fixation cells 200 ms before the onset of
the 50° saccade. As activity began in the buildup cell layer and then later in the burst
cell layer fixation-related activity in the rostral pole simultaneously diminished. At
saccade onset, fixation-related activity had ceased and cells in both layers of the caudal
SC were maximally active. The fixation cells began to discharge again at the end of the
Figure 3. Independence of burst cells from sequential activation. Each curve is for one cell which is located progressively further caudal in the SC as indicated by the dots on the SC map below. Activity was obtained when the monkey made 50° saccades. Optimal amplitude for each cell is indicated on the right. Same discharge is aligned on saccade onset (left column) and on saccade end (right column). Only cells in the most-caudal SC were activated during the 50° saccade. (After Munoz and Wurtz 1994b).

Thus the buildup cells differ from the burst cells in the activity contained in various parts of the movement map. In the burst cell layer, neural activity is maximal at saccade onset and diminishes in size during the saccade but does not spread across the motor map. In the buildup cell layer, the activity in the buildup cells seems to change as if a front of activity were moving across the SC during the course of the saccade. At the start of a large amplitude saccade, neural activity is centered in the caudal SC, but as the vector error between the current position of the visual axis and the target decreases during the saccade, cells located progressively more rostral in the SC (i.e., those preferring smaller and smaller amplitude gaze shifts) begin to discharge.
Figure 4. Successive activation of buildup cells whose fields are located progressively closer to the anterior pole of the SC. Same organization as Fig. 3. (After Munoz and Wurtz 1994b).

The difference in activity between the burst and buildup cells suggest that these cells play substantially different functions in the generation of saccades. Possible functions of these cells are presented in the chapter by Lance Optican in this Volume.

References


